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This paper reviews the significance and frequency of naturally occurring aneuploidy in higher plants. The role and mechanism of induction of aneuploidy by radiation, chemicals, thermal shocks, and self hybridization of polyploids and aneuploids in generating primary and secondary aneuploids is discussed. The utility of aneuploids in gene and chromosome transfer for plant improvement is reviewed.

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ANEUPLOIDY IN HIGHER PLANTS

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Abstract

This paper reviews the significance and frequency of naturally occurring aneuploidy in higher plants. The role and mechanism of induction of aneuploidy by radiation, chemicals, thermal shocks, and self hybridization of polyploids and aneuploids in generating primary and secondary aneuploids is discussed. The utility of aneuploids in gene and chromosome transfer for plant improvement is reviewed.

INTRODUCTION

Aneuploidy is a chromosome aberration in which an organism or a cell has either fewer or more chromosome(s) than the exact multiple of its haploid complement. An addition or deletion of an entire chromosome usually causes phenotypic alterations. In animals, aneuploidy brings about deleterious effects and depending upon the chromosome added or deleted, could be incompatible with life. Plants are less sensitive to chromosome imbalance than animals. Nevertheless, genomic imbalance in plants is accompanied by changes in their form and function. The relatively higher tolerance of aneuploidy in the plant kingdom has made plants a suitable material for the study of the mechanisms for the induction of aneuploidy and its utilization in genetic studies and plant improvement.

Plant geneticists were the first to discover the occurrence of aneuploids in the natural populations and to establish an association between aneuploidy and phenotypic alterations. Blakeslee (1) showed that in Datura stramonium globose shape of its capsules was accompanied by an addition to its chromosomal complement. He suggested the term 'trisomy' to indicate an addition of one chromosome to the diploid complement (2n+1). Similarly, loss of a chromosome from the basic chromosomal complement was termed as 'monosomy' (2n-1). Subsequently, monosomy was discovered in other plant species [e.g., Nicotiana tabaccum (2)] and in insects [e.g., Drosophila melanogaster (3)]. Further studies (4, 5, 6, 7) in plants showed that certain aneuploids had an extra isochromosome instead of an entire extra chromosome. Such aneuploidies were termed as 'secondary trisomies.' Similarly, when the extra chromosome consisted of two arms of nonhomologous chromosomes, it was termed as 'tertiary trisome.' These terms were subsequently adopted by mammalian cytogeneticists

to denote the variation in chromosome numbers in organisms or in cells. With advances in cytogenetic techniques, very complex nomenclature has been developed to denote the addition to or loss of chromosome(s) from the basic chromosomal complement. A brief discussion of this nomenclature has been presented by Khush (8). Although secondary and tertiary trisomics have played an important role in understanding hereditary mechanisms and plant improvement, we have limited our comments in this review mainly to the origin and utilization of primary aneuploids. Excellent reviews (8, 9, 10, 11) on other topics related to the study of aneuploidy are available.

OCCURRENCE OF ANEUPLOIDY

Recent studies have indicated that the frequency of spontaneously occurring aneuploidy is much higher than was believed in the past. Recent studies have suggested that 8 to 9 percent of the sperm from normal human males may be aneuploid (12). Since aneuploidy for most of the chromosomes is incompatible with human life, embryos carrying such abnormalities abort, contributing to fetal wastage. In spite of the loss of human embryos during the early developmental stages, 0.3-0.5% of the live births are aneuploids.

In plants, spontaneously occurring aneuploidy has been studied only in a few species (8). However, its occurrence in segregating progenies of inter-varietal and interspecific hybrids, polyploid, and aneuploid genomes has been studied more frequently. As can be seen from the data in table 1 most of the studies on the occurrence of aneuploidy (induced by mechanisms other than chemical and physical agents) have been performed mainly on plant species of economic importance. The frequency of aneuploidy in normal disomics varies from 0.3 percent in Nicotiana sylvestris to 1-2 percent in Avena sativa. However, in segregating progenies of disomic and tetrasomic hybrids, the frequency of aneuploids was as high as 70.5 percent. About 50 percent of the progenies from triploids were aneuploids.

SOURCES OF ANEUPLOIDY

Spontaneously occurring aneuploids have been discovered in many plant species. Although a small fraction of the aneuploids may have arisen from mitotic malsegregation during embryonic development, it is believed that errors of the meiotic process (including nondisjunction) may be the major source of aneuploidy in plants. Complex events related to meiosis such as bivalent formation, pairing, crossing over, and segregation render cells vulnerable to errors resulting in aneuploidy. The mechanisms and casual agents which induce so-called spontaneous aneuploidy are probably similar to those used by geneticists and plant breeders to induce aneuploidy. These factors can be grouped into the following categories: (1) physical factors, (2) chemical contaminants, (3) intrinsic factors, and (4) other sources.

Physical Factors.--Cosmic radiation may be one of the important sources of naturally occurring aneuploidy. Both ionizing and nonionizing radiations have been known to cause gene mutation and chromosome breaks. It is conceivable that chronic exposure to low levels of radiation may be interfering with normal meiotic processes and produce n+1 and n-1 gametes. Usually radiation exposure is more effective in producing monosomies than trisomies. This perhaps is related to the clastogenic property of radiation. The mechanism by which radiation may cause aneuploidy is poorly understood. Khush and Rick (29) proposed that radiation may cause damage to the centromere and disrupt its normal activity; or radiation may cause damage by breaking chromatids and the formation of dicentric chromosomes, which may lead to chromosome loss. In addition to radiation, thermal shock has been known to interfere with normal pairing which may lead to aneuploidy. An excellent review on the role of physical agents in the induction of aneuploidy has been published by Bond and Chandley (30), and the reader is referred to this review for further details.

Chemical Contaminants.--A large number of manmade industrial chemicals, agricultural chemicals, drugs, industrial effluents and emissions are being introduced into our environment in steadily increasing concentrations. Plant life is the major recipient of this assault. Although the role of complex chemical environmental mixtures in inducing aneuploidy in plants has not been well documented, it is clear that several environmental chemicals are capable of inducing aneuploidy in plants (31). The role of chemicals in the etiology of aneuploidy was the subject of recent reviews (32, 33).

In addition to manmade pollutants, other potential sources of chemical pollution include: (a) volcanic eruptions, (b) incomplete combustion products and their chemical and biotransformation, (c) microbial activities, and (d) release of chemicals by plants. It is probable that these chemicals may be partially responsible for naturally occurring aneuploidy. Under a natural environment, chemicals with the ability to cause chromosome aberrations may be present in low concentrations. In fact, most chemicals which interfere with normal cell division processes are effective in causing aneuploidy only at low concentrations; at higher concentrations, these chemicals partially block cell division and induce polyploidy or cell death (34).

Intrinsic Factors.--The existence of meiotic mutants that promote non-disjunction in humans and rodents has been speculated (35, 36, 37). The mechanism by which these mutants cause aneuploidy in mammals is not well understood. However, these processes in plants, especially the genetics of the pairing behavior during meiosis, have been well understood and documented. There are intervarietal and interspecific differences with regard to the frequency with which asynaptic and desynaptic genotypes occur in nature. Such asynaptic and desynaptic genotypes produce large numbers of univalents at metaphase 1. Such univalents produce n+1 and n-1 gametes at random which

upon fertilization with normal gametes yield trisomic and monosomic sporophytes. Trisomics were isolated from asynaptic progenies of N. sylvestris (7), Pisum sativum (38), capsicum annum (39), and from other plant species. In addition to trisomics, monosomics have been isolated from asynaptic and desynaptic strains of tobacco (40), wheat (41), cotton (42), and tetraploid species of Avena (43).

Other sources.--The polyploid species, particularly autotriploids, have been a proficient source of primary trisomics and monosomics. Because of the pairing irregularities at meiosis, triploids produce gametes varying in chromosome number. The selfed progenies of such triploids have yielded primary trisomics in all major plant species that have been studied (8).

Among polyploid species, the occurrence of aneuploids is not limited to autotriploids; plants with aberrant chromosome number have been isolated from autotetraploids, probably by the development of 2n+1 or 2n-1 gametes through the process of parthenogenesis. Formation of the restitution nuclei caused by the failure of first division at meiosis may cause the formation of gametes with unequal numbers of chromosomes. There is usually a higher degree of nondisjunction in genomes with aneuploid chromosomes. Relatively higher degrees of irregularities of chromosome distribution during the meiotic process in the trisomes and monosomes further gives rise to nonparental types of aneuploids. Thus, nonparental types of aneuploids have been isolated from primary trisomics, tertiary trisomics, multiple trisomics, and translocation heterozygotes. Haploids, too, have proved to be a reliable source for the recovery of aneuploidies.

Intervarietal and interspecific crosses are another proficient source of aneuploids, especially monosomics.

UTILITY OF ANEUPLOIDS IN PLANT IMPROVEMENT AND LINKAGE STUDIES

Knowledge of mode of inheritance of characters of economic importance and location of genes on chromosomes responsible for these traits is a fundamental requirement for planned plant improvement work. Aneuploids in plants have not only been used as one of the ways for getting information on the location of genes and their linkage relationships, but also as direct aids in plant breeding as well.

Various aneuploids such as trisomics, monosomics, and nullisomics have been used in different crop species to assign genes to the critical chromosome involved in these aneuploids and to construct linkage maps. Genetic stocks with normal chromosome numbers but having chromosomal abnormalities, such as duplications representing partial trisomy or tetrasomy and deletions representing partial monosomy or nullisomy are also a good source of locating genes in chromosomes. The information on gene location makes chromosome transfer technique very effective for incorporating economically useful characters, particularly when conditions are not favorable for the expression of the character.

Tertiary trisomics, where the extra chromosome is a translocation chromosome, can be used in the production of hybrid seed in conjunction with genetic male sterility. This procedure overcomes the need for restoring fertility which is required while using cytoplasmic-genetic male sterility. Ramage and Tuleen (44) have described the use of such a stock in the production of hybrid barley.

Monosomies are used in the transfer of a chromosome carrying desirable genes from one variety to another lacking the character in question. This has been done in wheat by producing substitution lines (45, 46, 47). This

method is very helpful in improving the existing adapted varieties. To improve a variety in characters controlled by genes on the same chromosome, the substitution method is quicker and more efficient than the conventional breeding methods. The application of substitution lines has been found to be more effective in allopolyploids because the chromosome being substituted has no opportunity to cross over with its homolog during the transfer (48). The use of substitution lines to study hybrid vigor was suggested by Sears (49) by using reciprocal substitutions of the two varieties whose hybrid displays heterosis.

Thus, aneuploidy in plant species, whether naturally occurring or induced through genetic manipulations, has been employed by geneticists and plant breeders for understanding mechanisms of chromosome segregation and plant improvement.

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Table 1. Frequency of aneuploids in natural populations and in segregating progenies

Species	Aneuploid	Recovery source	Frequency (percent)	Reference
Avena sativa	2n-1	Disomic	0.42	13
Avena sativa	2n-1	Disomic	1.15	14
Capsicum annum	2n+1	Haploid	1.96	15
Corchorus species	2n+1	Interspecific hybrids	8.60	16
Datura stramonium	2n+1	Haploids	3.05	17
Datura stramonium	2n+1	Disomic	0.16	18
Datura stramonium	2n+1	Primary trisomics	0.80	18
Datura stramonium	2n+1	Disomic x tetrasomic	70.5	18
Datura stramonium	2n+1	Tetrasomic x disomic	63.9	18
Datura stramonium	2n+1	Tetrasomic x tetrosomic	49.3	18
Gossypium barbadense	2n-1	Haploid	0.24	19
Hordenm vulgare	2n+1	Triploid	59.0	20
Lycopersicum esculantam	2n+1	Triploid	42.7	21
Nicotiana sylvestris	2n+1	Disomic	0.3	22
Nicotiana sylvestris	2n+1	Asynaptic	4.4	22
Nicotiana tabacum	2n-1	Haploid x disomic	43.6	7
Pennisetum typhoid	2n+1	Triploid	41.6	23
Pennisetum typhoid	2n+1	Triploid x diploid	22.0	23
Pennisetum typhoid	2n+1	Diploid x triploid	2.1	23
Secale cereale	2n+1	Triploid	39.7	24
Sorgham vulgare	2n+1	Haploid	1.3	25
Triticum aestivum	2n-1	Disomic	1.1	26
Triticum species	2n-1	Interspecific hybrids	29.2	27
Zea maize	2n+1	Autotetraploid	0.005	28